

RESPONSE STRATEGIES OF ADULT MALE
SCHIZOCOSA CRASSIPES (ARANEAE: LYCOSIDAE)
DURING AGONISTIC INTERACTIONS¹

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INTRODUCTION

This paper represents one of a series (Aspey, 1975a, b, 1976a,b,c) on the ethology and behavioral ecology of the brush-legged wolf spider *Schizocosa crassipes* (Walckenaer). Among lycosids, the adult males of this species are unusual in that they exhibit an elaborate and extensive behavioral repertoire during agonistic interactions (Aspey, 1976b). As immatures, the spiderlings exhibit a characteristic leg wave display that spaces conspecifics and presumably minimizes cannibalism (Aspey, 1975a). As adults, the males develop black foreleg brushes and exhibit the complex behaviors seen exclusively during adult male-male agonistic interactions. This display is primarily a visually-mediated communication system that preserves the personal space of adult males (Aspey, 1976c).

These spiders are found in dense abundance among leaf litter at the forest-meadow interface, and share characteristics typical of "edge" species (Aspey, 1976a). Furthermore, males are more active than females, and in the natural habitat during a given one-minute observation period, an adult male is likely to encounter three males to one female. By exhibiting one or more of the foreleg movements and/or postures comprising the behavioral repertoire, certain males drive other males away from the female while remain-

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ing in the female's vicinity. Thus, the extensive agonistic behavioral repertoire may also confer a mating advantage to those males most successful in driving other males away from the female.

Although this hypothesis has not yet been demonstrated experimentally, the males do exhibit stable, linear dominance-subordination relations among themselves when tested in the laboratory under varying social, spatial, and population densities (Aspey, 1975b, 1976b,c). Using a variety of analytical and descriptive techniques, each adult male *S. crassipes* can be classed as Dominant, Intermediate, or Subordinate in terms of the kinds and frequencies of agonistic behaviors exhibited during male-male encounters. Although the dominance classification is based on one animal's responses to an opponent (i.e., inter-individual behaviors), this study demonstrates that strikingly different response strategies are also adopted by Dominant and Subordinate spiders when intra-individual behavior sequences are analyzed

METHODS

Subjects

The subjects were 40 adult males of the ground-dwelling brush-legged wolf spider *Schizocosa crassipes* (Walckenaer) (body length = 7-10 mm; carapace width = 3-4 mm; leg span = 27-30 mm). Molting to the adult occurs in late May, at which time the males develop conspicuous tufts of black hairs on the tibiae of the forelegs, with smaller brushes on the patellae. The spiders were collected as immatures among leaf litter in early May at Stroud's Run State Park, Athens, Ohio, U.S.A., and housed individually in visually-isolated, covered plastic containers (12.5 × 7.0 × 7.0 cm) until 1 wk after the final molt. Seven to ten days after the final molt each spider was marked with nontoxic enamel paint ("Pactra 'namel," Los Angeles, CA) on the dorsal surface of the cephalothorax and/or abdomen. No detrimental behavioral effects were apparent following paint application.

All spiders were tested in four groups each of two, three, or five spiders matched into size categories of 0.5 mm increments based on adult carapace width (Hagstrum, 1971). Behavioral observations were made in various sized rectangular glass terraria (90, 180, 270, or 540 cm² floor space) having paper substrata strewn with

dried leaves. Three of the four glass walls of each terraria were shielded with white paper on the outside to minimize external visual distractions. Each terrarium was covered with glass to prevent escape and to maintain relatively constant humidity conditions ($24.5^{\circ}\text{C} \pm 1.0$ SD; 60.0% R.H. ± 2.0 SD). Water was available *ad libitum* from cotton-plugged vials, and food consisted of larvae of the yellow mealworm beetle *Tenebrio molitor* offered twice weekly. Photoperiod consisted of 16-17 hr of continuous artificial light alternated with 7-8 hr of continuous darkness.

Data Collection

Observations were conducted from early June through late July, 1973, and data collection began 5-7 days following marking of the animals. Each observation terrarium rested on a styrofoam block placed on a separate table from the recording equipment to reduce vibrations, and I was positioned 45 cm in front of the chamber. Protocol during all male-male interactions was tape-recorded and data were transcribed at a later date. Following transfer to the observation terrarium, subjects were observed for 10 consecutive days at approximately the same time. The frequencies of each behavior comprising the agonistic behavioral repertoire of *S. crassipes* during adult male-male interactions (Aspey, 1976b) were recorded continuously throughout the observation period. Since the duration of each observation period varied with the number of spiders present (with $N=2$ the observation period lasted 20 min; with $N=3$, 25 min; with $N=5$, 35 min), the data were adjusted to yield mean frequencies of each behavior per 20 min.

An interaction was considered to occur when one spider approached within 3-5 cm of another spider; data were discarded when two spiders simply passed one another without orienting or displaying to one another. An interaction was considered to continue when one spider chased or pursued a retreating spider. An interaction was considered terminated if an animal fled or was actively driven away by another spider. An interaction was considered to involve only two spiders because interactions among three or more spiders occurred only twice.

Transitional Probabilities

To determine predictable behavior sequences for individual spiders, an intra-individual transition probability matrix was con-

structured in which the preceding acts are listed as the horizontal rows and the following acts are listed as the vertical columns (Table I).

Such a matrix indicates how frequently given behaviors immediately follow or precede other specific behaviors, and similar techniques have been employed by a variety of investigators (Andrew, 1956; Altmann, 1965; Hazlett and Bossert, 1965; Delius, 1969; Wilson and Kleiman, 1974). The construction of an inter-individual transition probability matrix to determine which behaviors were exhibited by one spider in response to another's behavior is discussed in Aspey (1976b). Although procedures for constructing the intra-individual transition probability matrix of the present study are fundamentally the same as for the inter-individual transition probability matrix (Aspey, 1976b), no attention was paid in this analysis to acts performed by other spiders and their possible influence. To obtain the matrix, the complete sequence of agonistic behaviors was broken down into a series of two-act sequences. To illustrate, the four-act sequence Jerky Tapping — Following Walk — Oblique Extend — Vibrate-Thrust, provided three two-act sequences: Jerky Tapping — Following Walk, Following Walk — Oblique Extend, and Oblique Extend — Vibrate-Thrust.

To determine when any two behaviors performed by the same spider were significantly linked beyond chance expectation, the method developed by Andrew (1956) and employed by McKinney (1961) and Wilson and Kleiman (1974) was used. Two behaviors were considered significantly linked if the difference between the observed and expected values was greater than three times the square root of the expected value. In other words, the square root of the observed value was estimated as the standard error of the expected value, and a difference of more than three times the standard error between the obtained and expected totals was regarded as significant with a deviation of 2.58 times the standard error corresponding to $p < 0.01$ level of significance. With large samples the distribution was the same as for chi-square; however, Andrew's method was not restricted by the assumptions of chi-square, namely it: (1) did not assume independence of each variable; (2) allowed expected frequencies of zero; and (3) allowed expected frequencies for five or fewer in more than 20% of the cells. Therefore, Andrew's method had the same power as chi-square but allowed for the analysis of infrequently occurring behaviors, and did not assume that all

Table I: Transitional probabilities of agonistic behaviors occurring during intra-individual sequences in adult male *Schizocosa crassipes*. Underlined transitions departed significantly ($p < 0.01$) from the null order model. List of abbreviations: Ap = Approach; FA = Front Approach; FW = Following Walk; Cs = Chase; MA = Mutual Avoid; Rt = Retreat; Rn = Run; Ct = Contact; WA = Wave and Arch; PW = Prolonged Wave; JT = Jerky Tapping; HE = Horizontal Extend; OE = Oblique Extend; VE = Vertical Extend; UD = Up-Down; VT = Vibrate-Thrust. Consult Aspey (1976b) for a complete description of each behavior.

Following Behaviors

Initial Behaviors	Ap	FA	FW	Cs	MA	Rt	Rn	Ct	WA	PW	JT	HE	OE	VE	UD	VT	Total	N
Ap	(-) <u>.020</u>	.000	.011	<u>.032</u>	.028	<u>.049</u>	<u>.006</u>	<u>.062</u>	.118	<u>.001</u>	<u>.428</u>	.081	.063	.044	.037	<u>.020</u>	1.000	2172
FA	.000	.000	.000	.000	<u>.143</u>	.143	.024	.071	.190	.024	<u>.000</u>	<u>.071</u>	<u>.238</u>	.000	.071	.024	1.000	42
FW	.000	.000	<u>.043</u>	.043	.000	.014	.007	.029	.071	.000	<u>.657</u>	.050	.029	.000	.021	.036	1.000	140
Cs	.020	.000	.020	<u>.190</u>	<u>.030</u>	.070	.020	.030	.110	.000	.310	.010	.020	.000	.010	<u>.160</u>	1.000	100
MA	.000	.000	.000	.000	.000	.000	.000	.000	.333	.000	.667	.000	.000	.000	.000	.000	1.000	3
Rt	<u>.294</u>	.000	<u>.059</u>	.012	.000	.000	.000	.012	.235	.000	.294	.000	.047	.000	.024	.024	1.000	85

Rn	.417	.000	.000	.000	.042	.167	.000	.125	.000	.083	.000	.083	.000	.083	.000	.083	.000	24
										(-)								
Ct	.040	.000	.007	.020	.450	.146	.026	.020	.073	.000	.007	.060	.113	.013	.026	.000		151
										(-)	(-)	(-)	(-)	(-)	(-)			
WA	.066	.000	.010	.018	.043	.120	.007	.031	.198	.001	.171	.168	.066	.013	.054	.031		667
PW	.065	.000	.000	.032	.032	.000	.000	.000	.710	.097	.032	.032	.000	.000	.000	.000		31
										(-)	(-)	(-)	(-)	(-)	(-)			
JT	.076	.003	.023	.040	.014	.092	.008	.060	.016	.003	.336	.050	.062	.004	.031	.052		1091
										(-)	(-)							
HE	.030	.006	.000	.006	.000	.107	.115	.006	.071	.305	.000	.044	.041	.104	.018	.148		338
										(-)	(-)							
OE	.013	.027	.000	.013	.007	.103	.240	.007	.130	.123	.000	.030	.140	.050	.023	.933		300
										(-)	(-)							
VE	.188	.000	.000	.000	.031	.125	.344	.000	.063	.125	.000	.031	.031	.031	.000	.031		52
										(-)	(-)	(-)	(-)	(-)	(-)	(-)		
UD	.005	.028	.000	.014	.009	.065	.144	.000	.051	.209	.000	.037	.177	.167	.019	.074		215
											(-)	(-)	(-)	(-)	(-)	(-)		
VT	.020	.030	.020	.000	.020	.040	.200	.030	.010	.100	.000	.210	.100	.120	.020	.080		100
Expected Value	.043	.004	.013	.030	.035	.076	.038	.044	.125	.042	.285	.276	.072	.038	.034	.045		5491

Table I: Transitional probabilities of agonistic behaviors occurring during intra-individual sequences in adult male *Schizocosa crassipes*. Underlined transitions departed significantly ($p < 0.01$) from the null order model. List of abbreviations: Ap = Approach; FA = Front Approach; FW = Following Walk; Cs = Chase; MA = Mutual Avoid; Rt = Retreat; Rn = Run; Ct = Contact; WA = Wave and Arch; PW = Prolonged Wave; JT = Jerky Tapping; HE = Horizontal Extend; OE = Oblique Extend; VE = Vertical Extend; UD = Up-Down; VT = Vibrate-Thrust. Consult Aspey (1976b) for a complete description of each behavior.

Initial Behaviors	Following Behaviors																	Total	N		
	Ap	FA	FW	Cs	MA	Rt	Rn	Ct	WA	PW	JT	HE	OE	VE	UD	VT					
Ap	(-)					(-)	(-)		(-)							(-)				1.000	2172
	<u>.020</u>	.000	.011	.032	.028	<u>.049</u>	<u>.006</u>	<u>.062</u>	.118	<u>.001</u>	<u>.428</u>	.081	.063	.044	.037	<u>.020</u>					
FA	.000	.000	.000	.000	<u>.143</u>	.143	.024	.071	.190	.024	<u>.000</u>	.071	<u>.238</u>	.000	.071	.024				1.000	42
FW	.000	.000	<u>.043</u>	.043	.000	.014	.007	.029	.071	.000	<u>.657</u>	.050	.029	.000	.021	.036				1.000	140
Cs	.020	.000	.020	<u>.190</u>	.030	.070	.020	.030	.110	.000	.310	.010	.020	.000	.010	<u>.160</u>				1.000	100
MA	.000	.000	.000	.000	.000	.000	.000	.000	.333	.000	.667	.000	.000	.000	.000	.000				1.000	3
Rt	<u>.294</u>	.000	<u>.059</u>	.012	.000	.000	.000	.012	.235	.000	.294	.000	.047	.000	.024	.024				1.000	85
Rn	.417	.000	.000	.000	.000	.042	<u>.167</u>	.000	.125	.000	.083	.000	.083	.000	.083	.000				1.000	24
Ct	.040	.000	.007	.020	<u>.450</u>	<u>.146</u>	.026	.020	.073	.000	<u>.007</u>	.060	.113	.013	.026	.000				1.000	151
WA	.066	.000	.010	.018	.043	<u>.120</u>	<u>.007</u>	.031	<u>.198</u>	<u>.001</u>	<u>.171</u>	<u>.168</u>	<u>.066</u>	<u>.013</u>	.054	.031				1.000	667
PW	.065	.000	.000	.000	.032	.032	.000	.000	.000	.710	.097	.032	.032	.000	.000	.000				1.000	31
JT	<u>.076</u>	.003	.023	.040	<u>.014</u>	.092	<u>.008</u>	.060	.016	<u>.003</u>	<u>.336</u>	<u>.050</u>	.062	<u>.004</u>	.031	.052				1.000	1091
HE	.030	.006	.000	.006	<u>.000</u>	<u>.107</u>	<u>.115</u>	<u>.006</u>	.071	<u>.305</u>	<u>.000</u>	<u>.044</u>	.041	<u>.104</u>	.018	<u>.148</u>				1.000	338
OE	.013	<u>.027</u>	.000	.013	.007	.103	<u>.240</u>	<u>.007</u>	.130	<u>.123</u>	<u>.000</u>	<u>.030</u>	<u>.140</u>	.050	.023	<u>.933</u>				1.000	300
VE	<u>.188</u>	.000	.000	.000	.031	.125	<u>.344</u>	.000	.063	.125	<u>.000</u>	.031	.031	.031	.000	.031				1.000	32
UD	.005	<u>.028</u>	.000	.014	.009	.065	<u>.144</u>	<u>.000</u>	<u>.051</u>	<u>.209</u>	<u>.000</u>	<u>.037</u>	<u>.177</u>	<u>.167</u>	.019	.074				1.000	215
VT	.020	<u>.030</u>	.020	.000	.020	.040	<u>.200</u>	.030	<u>.010</u>	.100	<u>.000</u>	.210	.100	<u>.120</u>	.020	.080				1.000	100
Expected Value	.043	.004	.013	.030	.035	.076	.038	.044	.125	.042	.285	.276	.072	.038	.034	.045				1.000	5491

variables were necessarily independent. Underlined transitions in Table I indicate those behaviors linked to one another which departed significantly ($p < 0.01$) from the null order model. Negative linkages are marked (-), indicating that certain behaviors occurred less frequently than expected by chance.

RESULTS

Transitional Probabilities

A total of 3,525 adult male-male agonistic interactions were recorded in the laboratory that included 14,109 behavioral acts. The original 20 agonistic behaviors were found to be better represented by 16 behavior categories, and the rationale for this consolidation is discussed in Aspey (1976b). When the data were cast into a 16×16 matrix, the occurrence of significant deviations from expected frequencies suggested a probabilistic structure to the intra-individual agonistic behavior sequences (Table I). Of 256 possible linkages from a 16×16 matrix, 37 occurred more frequently than expected by chance, while 30 occurred less frequently. With regard to only the foreleg movements and postures exhibited during agonistic interactions (Aspey, 1976b), a wider variety of subsequent behaviors occurred during intra-individual sequences than during inter-individual behavioral responses. For example, during intra-individual sequences, an average of 5.6 different agonistic behaviors followed a given foreleg movement or posture beyond chance levels, while only 2.6 different behaviors followed a given foreleg movement or posture during inter-individual encounters (Aspey, 1976b).

Sequential Behaviors of Dominant and Subordinate Spiders

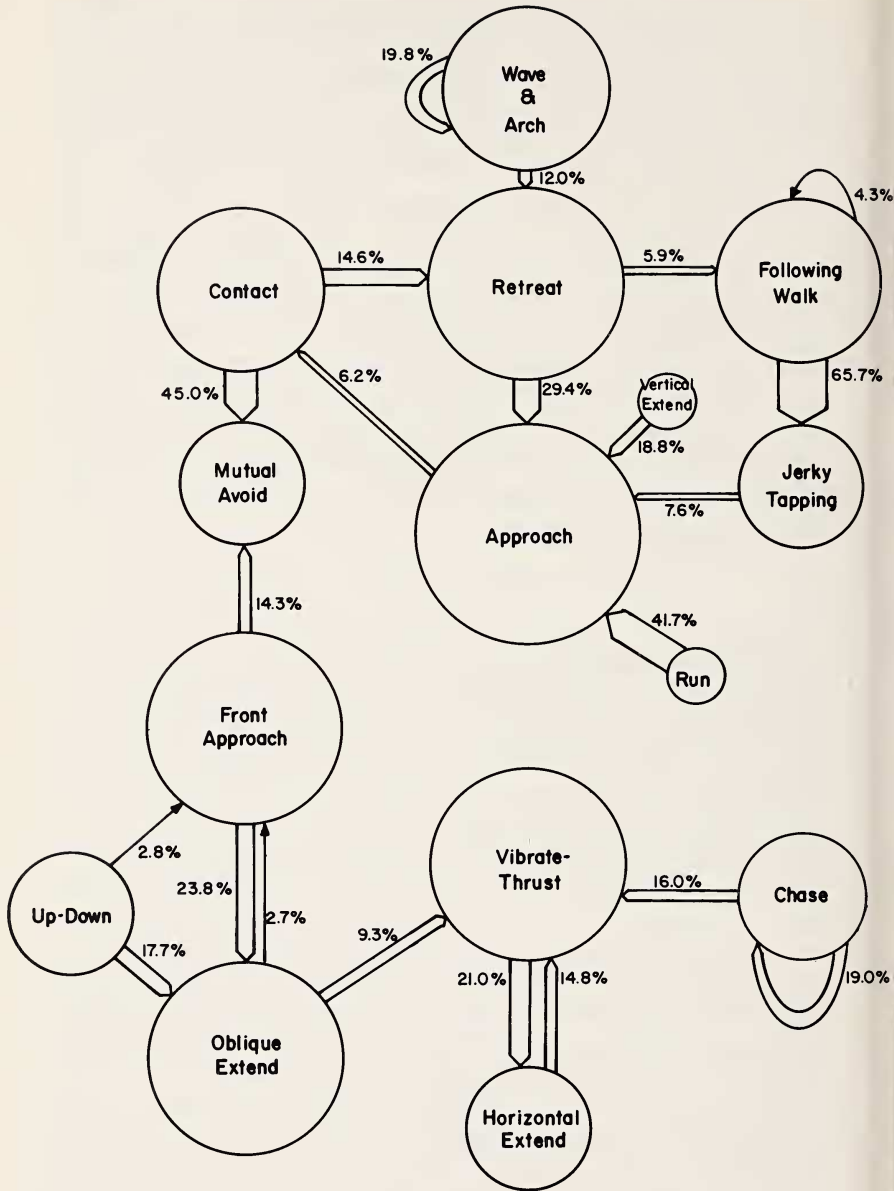
Since adult *S. crassipes* could be characterized as Dominant or Subordinate on the basis of the kinds and frequencies of agonistic behaviors exhibited during male-male interactions (Aspey, 1975b, 1976b), profiles of Dominant and Subordinate spiders were constructed using intra-individual behavior sequences. Although the original dominance classifications of the spiders utilized responses from one spider toward another, this method of characterizing Dominant and Subordinate spiders emphasized behavioral sequences exhibited by individual spiders.

Intra-individual behavioral sequences are diagrammed separately for the 16 Dominant spiders (Figure 1) and 16 Subordinate spiders (Figure 2). Dominant spiders were characterized by those agonistic behaviors comprising Factor I (Approach/Signal) and Factor II (Vigorous Pursuit) of Aspey's (1976b) factor analytic classification. Subordinate spiders were characterized by Run, Retreat, and Vertical Extend, those behaviors comprising Factor III (Run/Retreat) of Aspey's (1976b) factor analysis of the agonistic behavioral repertoire. A comparison of the original 20 behaviors displayed by Dominant and Subordinate spiders revealed that Dominant spiders exhibited a wider variety of behaviors linked together (15 out of a possible 20) than did Subordinate spiders (10 out of 20). Thus, these results indicate that Dominant and Subordinate spiders can not only be reliably identified on the basis of responses made by conspecifics toward them during agonistic interactions (Aspey, 1976b), but also by the response strategy exhibited during intra-individual behavior sequences.

DISCUSSION

A transition probability matrix of agonistic behaviors exhibited during adult male-male interactions in *S. crassipes* indicated that a wider variety of responses followed any given behavior by a single spider during intra-individual sequences than during inter-individual encounters (Aspey, 1976b). However, examination of Table I revealed that some of the sequential responses appeared inconsistent (e.g., Run or Vibrate-Thrust following the performance of Horizontal Extend; Run or Front Approach following the performance of Vibrate-Thrust). Horizontal Extend and Vibrate-Thrust are signal and active pursuit behaviors, routinely followed by some form of retreat during inter-individual encounters (Aspey, 1976b). However, if an animal exhibited Horizontal Extend or Vibrate-Thrust, seemingly aggressive behaviors, why would it suddenly retreat immediately after performing such a behavior?

Further analysis examining each specific spider indicated that some spiders were consistently Dominant over all partners, while others were consistently Subordinate to every partner. For example, Dominant spiders not only performed Horizontal Extend or Vibrate-Thrust more frequently, but also continued to exhibit Vigorous Pursuit behaviors if an initial encounter with a conspecific



did not result in that animal's retreating. If Subordinate spiders performed Vibrate-Thrust or Horizontal Extend, they then reverted to retreating, avoidance behaviors. When transition probabilities were examined separately for Dominant and Subordinate spiders, striking differences in response strategies were evident. Although eight Intermediate spiders were also identified (Aspey, 1976b), a meaningful kinematic diagram of their intra-individual response strategy could not be constructed with so few spiders. However, Intermediate spiders were typically approach-oriented, and made Contact preliminary to resolving rank differences with Dominant opponents. With Subordinate opponents, Intermediate spiders exhibited Oblique Extend, the only time a foreleg posture characteristic of Dominant spiders was exhibited (Aspey, 1976b).

If these intra-individual behavior sequences reflect a spider's responsiveness to its own behavior (i.e., feedback), then Dominant spiders exhibit the potential for more versatile response strategies during agonistic interactions than Subordinate spiders, presumably allowing greater flexibility when responding to conspecifics. Hazlett and Estabrook (1974a,b) also reported similar results regarding the response behavior of winning animals. Thus, Dominant and Subordinate spiders can not only be reliably identified on the basis of responses made by conspecifics toward them during agonistic interactions, but also by the response strategy exhibited during intra-individual behavior sequences.

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Fig. 1. [opposite] Transitional probabilities during intra-individual behavior sequences in Dominant adult male *Schizocosa crassipes*. Arrows connecting the agonistic behaviors represent significant linkages ($p < 0.01$) between and among the behaviors. The relative thickness of the arrows indicates the percent of time one agonistic behavior followed another. The relative size of each circle represents the number of different behaviors significantly linked with that behavior. Descriptions of the behaviors are given in Aspey (1976b).